Optimum mating systems for the myostatin locus in cattle

J. W. Keele[1] and S. C. Fahrenkrug

USDA, ARS, Roman L. Hruska U.S. Meat Animal Research Center, Clay Center, NE 68933-0166

ABSTRACT: Inactive myostatin (one or two copies) results in increased muscularity, increased yield of closely trimmed retail product, reduced fat content, increased lean growth efficiency, reduced quality grade, increased birth weight, and increased dystocia. Even though one or two copies of inactive myostatin reduces quality grade or marbling compared to zero copies, there is no decrease in meat tenderness. It may be possible to use mating systems to make the most of the advantages of inactive myostatin while minimizing the disadvantages. The objective of this study was to develop a method to compare mating systems among genotypes at the myostatin locus. Economic variables that influence the profitability of alternative mating systems are prices per unit of retail product for USDA quality grades Standard, Select, and Choice; cost of an assisted calving; and cost of genotyping. Because of variation in both economic variables and biological parameters, a single mating system is not expected to universally maximize profit. We identified seven mating systems that each yield maximum profit for different combinations of values for biological parameters and economic variables. Use of inactive myostatin was profitable as long as the price for Select was at least 80% of the Choice price and the price for Standard at least 60%. As the price for Select and Standard increase up to the Choice price, mating systems that produce a higher proportion of inactive myostatin alleles become more profitable. Profitable use of inactive myostatin depends either on retaining ownership of beef until it is fabricated into retail product or the development of specialty markets that place greater value on lean yield and less on marbling, unlike conventional U. S. markets.

Key Words: Double Muscling, Genetic Markers, Leanness, Mating Systems

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Introduction

Five different mutations have been identified in the bovine myostatin gene that result in an inactive gene product and double muscling (Kambadur et al., 1997; McPherron and Lee, 1997; Grobet et al., 1998). Hence, myostatin alleles can be aggregated into two functional classes: inactive myostatin (**mh**) and active myostatin (+). Cattle with one or two copies of mh exhibit increased muscling, reduced fat content, reduced marbling, increased meat tenderness, increased birth weight, and increased dystocia (Hanset et al., 1987; Wheeler et al., 1996; Casas et al., 1999).

Even though the discovery of double-muscling is not recent, use of mh to increase lean growth has been limited to a small fraction of the global cattle population. Widespread use of mh has apparently been constrained by unfavorable effects on dystocia and marbling.

Traditionally, it was thought that double muscling was inherited as an autosomal recessive and that +/+ and mh/+ conferred similar moderate phenotypes and mh/mh expressed an extreme phenotype. Before the development of markers for the myostatin locus, it was not possible to separate the difference between mh/+ and +/+ from breed differences at other loci. Recent genomics work has revealed that mh/+ confers substantial benefits to lean growth while having relatively modest effect on dystocia compared to +/+ (Casas et al., 1998, 1999). Recent advances in high-throughput genotyping (Higgens et al., 1997; Fahrenkrug et al., 1999) make it feasible to implement mating systems that were previously impossible. Knowledge of mh/+ vs +/+ phenotypic differences provides a reason to examine and possibly implement novel mating systems. The objective of this study was to develop a method to compare alternative mating systems making use of these developments.

Materials and Methods

Mating Systems

The proportion of the herd needed to generate replacement heifers is much larger than that needed for

[1]Correspondence: P. O. Box 166 (phone: 402/762-4251; fax: 402/762-4155; E-mail: keele@email.marc.usda.gov).

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Table 1. Possible matings among genotypes at the myostatin locus

Genotypes[a]			Genotypes of calves			Mating proportions[c]
Bulls	Cows	Mating[b]	mh/mh	mh/+	+/+	
mh/mh	mh/mh	22	1	0	0	P_{22}
	mh/+	21	0.5	0.5	0	P_{21}
	+/+	20	0	1	0	P_{20}
mh/+	mh/mh	12	0.5	0.5	0	P_{12}
	mh/+	11	0.25	0.5	0.25	P_{11}
	+/+	10	0	0.5	0.5	P_{10}
+/+	mh/mh	02	0	1	0	P_{02}
	mh/+	01	0	0.5	0.5	P_{01}
	+/+	00	0	0	1	P_{00}

[a]Alleles are mh for mutations leading to inactive myostatin and + for active protein.
[b]Matings are denoted by *ij* where *i* (0, 1, or 2) is the number of copies of inactive myostatin for the sire and *j* for the dam.
[c]Mating proportions are denoted by P_{ij} which is the proportion of the cow herd allocated to mating *ij* subject to $0 \le P_{ij} \le 1$ and $\sum_{i=0}^{2}\sum_{j=0}^{2} P_{ij} = 1$.

replacement of bulls. We consider mating systems that are sustainable in the sense that female replacements are produced within the herd but male replacements can be purchased. If replacement bulls are not available for purchase, they can be produced from a small number of additional matings without substantially modifying the composition of the herd.

All nine possible matings among genotypes at myostatin and proportions of progeny genotypes produced per mating are presented in Table 1. Alleles are mh for mutations leading to inactive myostatin and + for active protein. Mating systems are defined by the proportion of the herd allocated to each mating. Let P_{ij} denote the proportion of the herd allocated to mating *ij* where *i* (0, 1, or 2) is the number of copies of mh for the sire and *j* for the dam. We refer to mating systems as an ordered list of the matings included. For example, 20, 00 denotes a mating system with two matings, which include mh/mh bulls with +/+ cows and +/+ bulls with +/+ cows. Matings are listed in order of priority. Matings listed on the left are maximized relative to matings listed on the right.

Genotypic frequencies are $\boldsymbol{Z'P}$ for sires, $\boldsymbol{X'P}$ for dams, and $\boldsymbol{T'P}$ for calves, where

$$\boldsymbol{X'} = \begin{bmatrix} 1 & 0 & 0 & 1 & 0 & 0 & 1 & 0 & 0 \\ 0 & 1 & 0 & 0 & 1 & 0 & 0 & 1 & 0 \\ 0 & 0 & 1 & 0 & 0 & 1 & 0 & 0 & 1 \end{bmatrix},$$

$$\boldsymbol{Z'} = \begin{bmatrix} 1 & 1 & 1 & 0 & 0 & 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & 1 & 1 & 1 & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 & 0 & 0 & 1 & 1 & 1 \end{bmatrix},$$

$\boldsymbol{P'} = [P_{22}\ P_{21}\ P_{20}\ P_{12}\ P_{11}\ P_{10}\ P_{02}\ P_{01}\ P_{00}]$ and

$$\boldsymbol{T'} = \begin{bmatrix} 1 & 0.5 & 0 & 0.5 & 0.25 & 0 & 0 & 0 & 0 \\ 0 & 0.5 & 1 & 0.5 & 0.5 & 0.5 & 1 & 0.5 & 0 \\ 0 & 0 & 0 & 0 & 0.25 & 0.5 & 0 & 0.5 & 1 \end{bmatrix} \text{(Table 1).}$$

Requiring adequate numbers of heifers to maintain herd size introduces the constraint

$$r\boldsymbol{X'P} \le \frac{bs}{2}\boldsymbol{T'P},$$

which is the same as

$$\beta\boldsymbol{X'P} \le \boldsymbol{T'P} \qquad [1]$$

where b is calves born per cow exposed to breeding, s is survival from birth to puberty or slaughter, r is replacement rate, and $\beta = \frac{2r}{bs}$ is the proportion of the cow herd that needs to be committed to the production of replacement heifers to maintain herd size. Constraints that arise strictly because P_{ij} are proportions are

$$0 \le P_{ij} \le 1 \text{ and } \sum_{i=0}^{2}\sum_{j=0}^{2} P_{ij} = 1. \qquad [2]$$

Profit

We assume that cattle are slaughtered at an age-constant end point. Marbling and closely trimmed retail product weight are not suitable end points currently because there is inadequate quantitative information describing how these traits change with age. There is no evidence of differences among myostatin genotypes for feed costs of cattle slaughtered at a constant age. In our model, we assume that feed costs are similar for all matings. Average profit plus fixed costs per cow is

$$\pi + c_f = (bs\boldsymbol{P'T} - r\boldsymbol{P'X})\boldsymbol{wQv} - b\boldsymbol{P'D}\boldsymbol{\delta}\boldsymbol{R}c_d - bs\boldsymbol{P'G}c_g \qquad [3]$$

where π is profit; c_f is fixed costs common to all mating systems;

$$\boldsymbol{w} = \begin{bmatrix} w_2 & 0 & 0 \\ 0 & w_1 & 0 \\ 0 & 0 & w_0 \end{bmatrix}$$

where w_i is kilograms of closely trimmed retail product for cattle with the i^{th} genotype;

$$\boldsymbol{Q} = \begin{bmatrix} Q_{21} & Q_{22} & Q_{23} \\ Q_{11} & Q_{12} & Q_{13} \\ Q_{01} & Q_{02} & Q_{03} \end{bmatrix}$$

where Q_{ik} is the probability that cattle with the i^{th} genotype receive the k^{th} (k = 1 for Standard, 2 for Select, and 3 for Choice) USDA quality grade;

$$\boldsymbol{v'} = [v_1 \; v_2 \; v_3]$$

where v_k is the price ($ US) per kilogram of closely trimmed retail product with the k^{th} USDA quality grade;

$$\boldsymbol{D'} = \begin{bmatrix} 1 & 0 & 0 & 0.5 & 0 & 0 & 0 & 0 & 0 \\ 0 & 0.5 & 0 & 0 & 0.25 & 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & 0.5 & 0 & 0 & 1 & 0 & 0 \\ 0 & 0.5 & 0 & 0 & 0.5 & 0 & 0 & 0.5 & 0 \\ 0 & 0 & 1 & 0 & 0 & 0.5 & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 & 0.25 & 0 & 0 & 0.5 & 0 \\ 0 & 0 & 0 & 0 & 0 & 0.5 & 0 & 0 & 1 \end{bmatrix};$$

$$\delta' = \begin{bmatrix} \delta_{221} & \delta_{211} & \delta_{121} & \delta_{111} & \delta_{101} & \delta_{011} & \delta_{001} \\ \delta_{222} & \delta_{212} & \delta_{122} & \delta_{112} & \delta_{102} & \delta_{012} & \delta_{002} \end{bmatrix}$$

where δ_{ijk} is the probability that calving assistance is required for calves with genotype i born to dams with genotype j in parity k (k = 1 is first parity and 2 is second and later parities);

$$\boldsymbol{R'} = [r \quad 1 - r];$$

c_d is the cost of one assisted calving;

$$\boldsymbol{G'} = [0 \;\; 0 \;\; 0 \;\; 0 \;\; 0.75 \;\; 1 \;\; 0 \;\; 1 \;\; 0];$$

and c_g is the cost of genotyping one animal for myostatin. Each row of $\boldsymbol{D}$ is the distribution of calf genotype − dam genotype combinations for a mating. There are seven calf genotype – dam genotype combinations possible; hence, there are 7 columns in $\boldsymbol{D}$. $\boldsymbol{G}$ contains the fraction of calves that need to be genotyped for each mating. No progeny need to be genotyped for matings 22, 20, 02, or 00 because these matings do not produce a mixture of genotypes. No progeny need to be genotyped for matings 21 and 12 because genotypes mh/mh and mh/+ can be visually distinguished from each other. Only 75% of the progeny need to be genotyped for 11 because 25% of the progeny are mh/mh and they can be visually distinguished from mh/+ and +/+. All of the progeny need to be genotyped for matings 10 and 01. The profit equation, Eq. [3], and constraints, Eq. [1] and [2], are linear in $\boldsymbol{P}$; hence, for a given set of biological parameters and economic variables, the maximum-profit mating system can be determined using linear programming.

Example Biological Parameter Values

A wide range of values is indicated for many of the parameters in the literature. For these parameters, we chose two values near each end of the range. However, there is not space to evaluate all possible combinations of parameter values, so we defined one of the values for each parameter as the reference value. When nonreference values were used, all other parameters were set to reference values. The choice of reference parameters was arbitrary. For calves born per cow exposed to breeding, we used b = 0.8 or 0.9 (reference). Freetly and Cundiff (1998) reported estimates ranging from 76 to 97% for F_1 first-calf heifers raised on different levels of nutrition. For survival from birth to slaughter or puberty, we used s = 0.80 or 0.94 (reference). Cundiff et al. (1998) reported estimates ranging from 89 to 96% for survival from birth to weaning. We chose a lower value of 0.8 instead of 0.89 to consider losses from weaning to puberty or slaughter. For replacement rate, we used r = 0.1 or 0.2 (reference). Azzam et al. (1990) reported estimates ranging from 13 to 23%. For kilograms of closely trimmed (0 cm) retail product, we used

$$\boldsymbol{w} = \begin{bmatrix} 265 & 0 & 0 \\ 0 & 225 & 0 \\ 0 & 0 & 205 \end{bmatrix} \text{(reference)}$$

where w_0 = 205 kg is based on a 550-kg steer with dressing percentage equal to 60% and percentage of closely trimmed (0 cm) retail product yield equal to 62%. Casas et al. (1998) estimated the difference between mh/+ and +/+ at 20 kg. T. L. Wheeler (personal communication) observed a difference of 60 kg between mh/mh and +/+. For USDA quality grade distributions, we used

$$\boldsymbol{Q^r} = \begin{bmatrix} 0.83 & 0.11 & 0.06 \\ 0.10 & 0.57 & 0.33 \\ 0.01 & 0.42 & 0.56 \end{bmatrix} \text{(reference) or}$$

$$\boldsymbol{Q^{nr}} = \begin{bmatrix} 0.31 & 0.60 & 0.09 \\ 0.01 & 0.31 & 0.68 \\ 0 & 0.15 & 0.85 \end{bmatrix}.$$

Casas et al. (1998) observed 1% Standard, 42% Select, and 56% Choice for +/+ and 10% Standard, 57% Select, and 33% Choice for mh/+. T. L. Wheeler (personal communication) observed 83% Standard, 11% Select, and 6% Choice for 18 mh/mh animals. Through use of alternative genetic background (i.e., breeds), length of feeding, or plane of nutrition, it is possible to alter the USDA quality grade distribution. For example, it is well established that if cattle are fed a high plane of nutrition for a longer period of time (albeit with increased costs), marbling increases and the percentage of cattle grading at least Choice increases. $\boldsymbol{Q}^r$ and $\boldsymbol{Q}^{nr}$ represent genetic backgrounds and production systems conferring low and high marbling. For rate of calving assistance by calf genotype, dam genotype and parity, we used

$$\delta^{r'} = \begin{bmatrix} 0.70 & 0.60 & 0.50 & 0.41 & 0.41 & 0.24 & 0.24 \\ 0.37 & 0.27 & 0.17 & 0.07 & 0.07 & 0.04 & 0.04 \end{bmatrix} \text{(reference)}$$

or

$$\delta^{nr'} = \begin{bmatrix} 0.60 & 0.50 & 0.45 & 0.43 & 0.43 & 0.13 & 0.13 \\ 0.10 & 0.08 & 0.05 & 0.01 & 0.01 & 0.01 & 0.01 \end{bmatrix}.$$

For +/+ calves born to mh/+ or +/+ dams, Casas et al. (1999) observed 24% requiring assistance during calving for first-calf-heifers and 4% for mature cows. For calves born to mh/+ dams, 17% more mh/+ calves required assistance compared to +/+ for first-calf-heifers, and this difference was 3% for mature cows (Cundiff et al., 1996; Casas et al., 1999). Casas et al. (1999) observed a difference in rate of dystocia between mh/mh calves and mh/+ born from mh/+ of 20%. Genetic backgrounds, the environment, and management factors influence the proportion of calvings requiring assistance. δ^{r} and δ^{nr} represent genetic backgrounds and production systems conferring high and low calving assistance requirements.

Example Values for Economic Variables

For price per kilogram of USDA Choice closely trimmed retail product, we used v_3 = 2.55, 3.55 (reference) or $4.55 per kilogram. Urner Barry's Yellow Sheet (2001) lists a price of $2.80 per kilogram of carcass. The corresponding price per kilogram of closely trimmed retail product would be $4.06/kg if 62% of the carcass is closely trimmed retail product and a 10% discount is charged to pay for the cost of slaughter and fabrication. This value is within the range of Choice prices that we considered. For price per kilogram of Standard and Select closely trimmed retail product, we used all values satisfying $0 \le v_1 \le v_2 \le v_3$. For cost of an assisted calving, we used c_d = $80 (reference) or $160. For cost of genotyping one animal, we used c_g = $5 (reference) or $15.

Avoiding Dystocia in First-Calf Heifers

For a few of the mating systems, it is possible to avoid most of the increase in dystocia caused by inactive myostatin alleles by manipulating heifer matings. For example, for mating system 20, 00, if heifers are always mated to +/+ bulls (00 mating) there is only a slight increase (≤ 3%) in dystocia for 20, 00 over 00 resulting from producing mh/+ calves from mature cows and mating proportions are not compromised. However, it is not possible to reduce dystocia through selecting bull genotypes for mh/+ cows because half the calves from mh/+ cows are mh/+ themselves and preventing mh/+ first-calf-heifers from producing mh/+ calves is not possible. To avoid complexity, we chose to assume that parity does not influence mating decisions.

Results and Discussion

Profitability

If $\beta \le 0.5$, the number of mating systems capable of maximizing profit is only 15 (00; 22; 21; 12; 10; 01; 11; 20, 11; 02, 11; 20,10; 20, 00; 02, 12; 02, 22; 20,01; 02, 21); hence, optimization reduces to a comparison of profit plus fixed cost among 15 mating systems. Conversely, if $\beta > 0.5$, many more mating systems need to be considered, and the best optimization approach that we know of is linear programming. For the values of economic variables and biological parameters considered, we identified only seven maximum-profit mating systems (00; 22; 21; 20, 00; 20, 01; 02, 21; 21, 12). For these mating

Table 2. Maximum-profit mating systems

Mating system[a]	Mating proportions	Genotypic proportions of calves[b]			Constraints
		mh/mh	mh/+	+/+	
00	$P_{00} = 1$	0	0	1	$0 \le \beta \le 1$
22	$P_{22} = 1$	1	0	0	$0 \le \beta \le 1$
21	$P_{21} = 1$	0.5	0.5	0	$0 \le \beta \le 0.5$
20, 00	$P_{20} = 1 - \beta$, $P_{00} = \beta$	0	$1 - \beta$	β	$0 \le \beta \le 1$
20, 01	$P_{20} = \frac{1}{1+2\beta}$, $P_{01} = \frac{2\beta}{1+2\beta}$	0	$\frac{1+\beta}{1+2\beta}$	$\frac{\beta}{1+2\beta}$	$0 \le \beta \le 1$
02, 21	$P_{02} = \frac{1}{1+2\beta}$, $P_{21} = \frac{2\beta}{1+2\beta}$	$\frac{\beta}{1+2\beta}$	$\frac{1+\beta}{1+2\beta}$	0	$0 \le \beta \le 1$
21, 12	$P_{21} = \frac{1}{2\beta}$, $P_{12} = \frac{2\beta-1}{2\beta}$	0.5	0.5	0	$0.5 < \beta \le 1$

[a]Mating systems are identified by a list of matings with each mating denoted *ij* where *i* (0, 1, or 2) is the number of copies of inactive myostatin for the sire and *j* for the dam.
[b]Alleles are inactive myostatin (mh) and active protein (+).

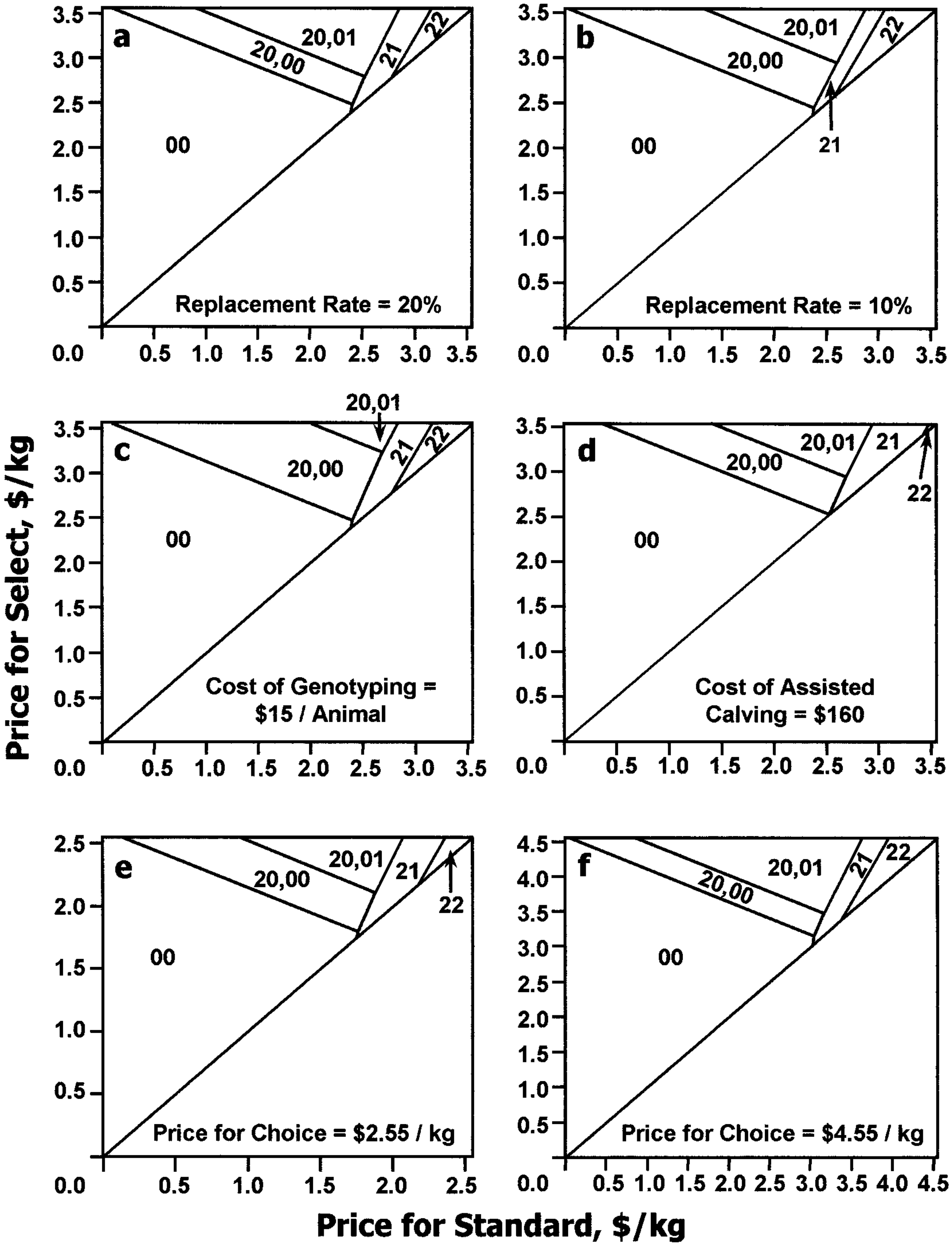

Figure 1. Regions within which particular mating systems yield maximum profit on the two-dimensional graph of USDA Select price (v_1) on the vertical axis and Standard price (v_2) on the horizontal. The Choice price (v_3) is fixed at the reference value of \$3.55/kg for all graphs except Figures 1e (v_3 = \$2.55/kg) and 1f (v_3 = \$4.55/kg). Price combinations falling below the diagonal line extending from ($v_1 = 0$, $v_2 = 0$) to (v_3, v_3) are null. Mating systems are identified by a list of matings with each mating denoted by *ij* where *i* (0, 1, or 2) is the number of copies of inactive myostatin for the sire and *j* for the dam. Figure 1a was generated using reference values for biological parameters and economic variables. Parameters and variables changed from reference values are indicated in the lower part of the graph.

systems, we present mating proportions, genotypic proportions, and constraints as a function of β (Table 2).

Presented in Figures 1 and 2 are regions within which particular mating systems yield maximum profit on the two-dimensional graph of USDA Select price on the vertical axis and Standard price on the horizontal. The Choice price is fixed at the reference value of \$3.55/kg for all graphs except Figures 1e (v_3 = \$2.55/kg) and 1f (v_3 = \$4.55/kg). All price combinations falling below the diagonal line extending from ($v_1 = 0$, $v_2 = 0$) to ($v_1 = v_3$,

$v_2 = v_3$) are null because $v_2 \geq v_1$. When reference values for biological parameters and economic variables were used (Figure 1a), mating system 00 maximized profit for all price combinations falling below the line extending from (v_1 = 0.038, v_2 = 3.55) to (2.38, 2.46). As Select and Standard prices increased toward the Choice price, mating systems yielding higher proportions of inactive myostatin became more profitable. Reducing the replacement rate from 20 to 10% (Figure 1a vs 1b) increased the region occupied by 22 at the expense of 21 and that of 20, 00 at the expense of 20, 01. Increasing the cost of genotyping from $5 per animal to $15 (Figure 1a vs 1c) increased the region occupied by 20, 00 at the expense of 20, 01. Increasing the cost of an assisted calving from $80 to $160 (Figure 1a vs 1d) increased the regions occupied by 00; 20,00; and 21 at the expense of 20, 01 and 22. Increasing the price of Choice from $2.55/kg to $4.55 (Figures 1a, 1e, and 1f) increased the regions occupied by 20, 01 and 22 at the expense of 00; 20, 00; and 21. Substituting $\boldsymbol{Q}^{nr}$ (high marbling) for $\boldsymbol{Q}^{r}$ (low marbling) (Figure 2a vs 1a) increased regions occupied by 20, 00; 20, 01; 21 and 22 at the expense of 00. Substituting δ^{nr} (low dystocia) for δ^{r} (high dystocia) increased regions occupied by 02, 21 and 22 at the expense of 21 and 20, 01. Reducing calves born per cow exposed to breeding from 90 to 80% increased the region occupied by 21, 12 at the expense of 21 and 22. With this change, 21, 12 emerged and 21 vanished because β > 0.5. Reducing survival from birth to puberty or slaughter from 94 to 80% increased regions occupied by 00 and 21, 12 at the expense of 22 and 21. With this change, both 22 and 21 vanished.

Marketing Options

Implicit in Eq. [3] is the assumption that producers receive payment per weight of closely trimmed retail

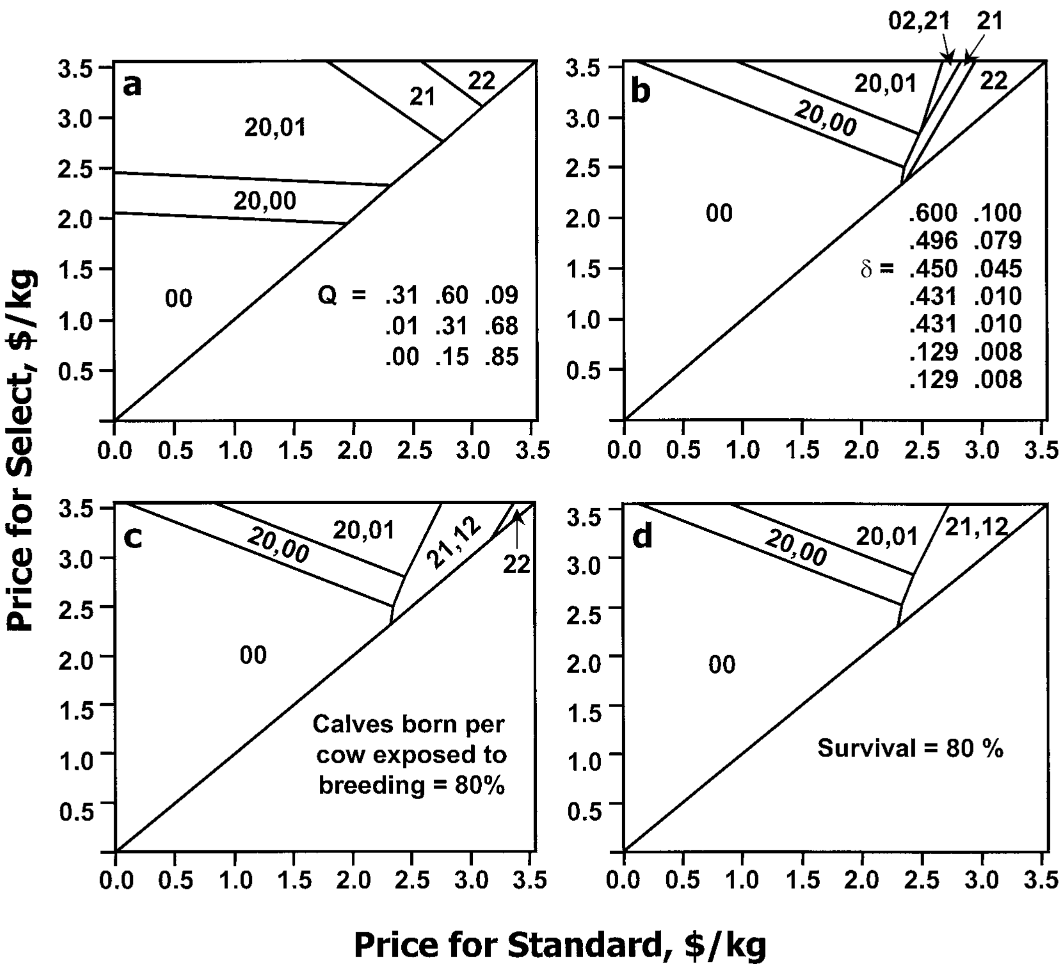

Figure 2. Regions within which particular mating systems yield maximum profit on the two-dimensional graph of USDA Select price (v_1) on the vertical axis and Standard price (v_2) on the horizontal. The Choice price (v_3) is fixed at the reference value of $3.55/kg for all graphs except Figures 1e (v_3 = $2.55/kg) and 1f ($v_3$ = $4.55/kg). Price combinations falling below the diagonal line extending from ($v_1 = 0$, $v_2 = 0$) to ($v_1 = v_3$, $v_2 = v_3$) are null. Mating systems are identified by a list of matings with each mating denoted by *ij* where *i* (0, 1, or 2) is the number of copies of inactive myostatin for the sire and *j* for the dam. Parameters and variables changed from the reference values used to generate Figure 1a are indicated in the lower part of the graph.

product. This is similar to a system in which producers retain ownership through fabrication of carcasses into retail cuts. The difference is that closely trimmed retail product is boneless, whereas retail cuts contain some bone. Specialty markets in which leanness is given greater value than marbling would favor inactive myostatin relative to conventional markets.

Preliminary data (T. L. Wheeler, unpublished data) indicate that a higher proportion of the carcass of cattle with inactive myostatin (mh/+ or mh/mh) is tender relative to +/+ beef. This would increase the value of conventionally lower-priced cuts (chuck and round) relative to middle meats (loin and rib) for cattle with inactive myostatin. Cattle with inactive myostatin have meat with higher tenderness even though their quality grades are lower than those of +/+ cattle (Wheeler et al., 1996). This indicates that mh/mh or mh/+ cattle should not be discounted for low quality grades and possibly should command higher prices than +/+. To accommodate pricing by genotype, substitute a vector containing prices for each genotype in place of $\boldsymbol{Qv}$ in Eq. [3]. Tenderness-based grading schemes (Shackelford et al., 1999) would favor inactive myostatin relative to conventional pricing based on USDA quality and yield grades.

Implications

High-throughput genotyping will make it feasible to implement novel mating systems among genotypes at the myostatin locus. We identified seven mating systems that maximize profit for different combinations of biological parameters and economic variables. Use of inactive myostatin may be profitable if producers retain ownership through fabrication to retail products. Marketing cattle based on conventional yield and quality grades does not favor use of inactive myostatin. Mating systems that use inactive myostatin yield maximum profit for most price combinations as long as discounts do not exceed 20% of the Choice price for Select and 40% for Standard. The profitability of inactive myostatin increases as prices for Standard and Select approach the Choice price.

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